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A diffusive plankton system with time delay and habitat complexity effects under Neumann boundary condition

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Abstract

In this paper, we establish a delayed semilinear plankton system with habitat complexity effect and Neumann boundary condition. Firstly, by using the eigenvalue method and geometric criterion, the stability of the equilibria and some conditions for determining the existence of Hopf bifurcation are studied. Through analyzing the stability of positive equilibrium, we found that at the positive equilibrium the system may switch finitely many times from stable to unstable, then from unstable to stable, finally becoming unstable, i.e., the time delay induces a "stability switch" phenomenon. Secondly, the properties of Hopf bifurcation are derived by applying the normal form method and center manifold theory, including the bifurcation direction and the stability of bifurcating periodic solutions. Finally, some numerical simulations are given to illustrate the theoretical results, and a biological explanation is given.

Keywords: Plankton; Marine habitat complexity; Time delay; Bifurcation; Diffusion system

1 Introduction

The plankton model is an important subject in marine biological systems. Chattopadhy et al. [1] showed that the delay of toxin release has a great impact on algal blooms. Wang [2] studied the toxic phytoplankton–zooplankton model and analyzed the effects of time delay and harvesting on the system. Sharma et al. [3] studied the plankton model with multiple delays. Roy et al. [4] established a nontoxic phytoplankton–zooplankton model and toxin-releasing phytoplankton–zooplankton model, respectively, and proved that nontoxic phytoplankton is beneficial to the growth of zooplankton, while toxin-producing phytoplankton is harmful to the growth of zooplankton. Furthermore, many scholars [5–7] have demonstrated that the toxins produced by phytoplankton can be used as a biological control quantity. Chattopadhayay et al. [8] pointed out that when the toxin rate exceeds the critical value, Hopf bifurcation occurs at the positive equilibrium. However, as long as the toxin rate is controlled close to the critical value, the system is stable at the positive equilibrium, so the harmful algal blooms are effectively controlled.

The theoretical study demonstrates [9–13] that the toxin released by phytoplankton may be a very strong regulation factor for the feeding rate of zooplankton. Habitat refers to the spatial scope of the environment where organisms appear, generally to the place where organisms live or the eco-geographical environment in which organisms live. The habitat complexity is the inhomogeneity of morphological characteristics within the structure itself and the heterogeneity of object arrangement in space. Research shows that the majority of population habitats are complex due to heterogeneity [14–16], for example, marine habitat become very complex in coral reefs, mangroves, sea grass beds, and salt marshes [17]. In lakes, the heterogeneity of habitat usually represents the vegetation depth and gradient diversity in coastal areas [18]. In addition, a large number of experimental studies show that habitat complexity reduces the encounter rate between predator and prey, thus reducing the predation rate [19–24]. Habitat complexity not only reduces the interaction between phytoplankton and zooplankton, but also reduces the available space of interacting species. Therefore, it is necessary to introduce habitat complexity into the plankton system.

Based on experiments and mathematical modeling, many scholars have established different mathematical models to describe the population dynamics [25–28]. Yang et al. considered the Holling type II plankton model with diffusion term in [29], and proposed the following model:

$$\begin{cases} \frac{\partial P(x,t)}{\partial t} = d_1 \Delta P + rP(1-\frac{P}{K}) - \frac{cfPZ}{a+\gamma P}, & x \in (0,\Omega), t>0, \\ \frac{\partial Z(x,t)}{\partial t} = d_2 \Delta Z + \frac{efP(t-\tau)Z}{a+\gamma P(t-\tau)} - \mu Z - e\rho P^{2/3} Z, & x \in (0,\Omega), t>0, \\ P_x(0,t) = Z_x(0,t) = 0, \quad P_x(\Omega,t) = Z_x(\Omega,t) = 0, & t>0, \\ P(x,0) = P_0(x) \geq 0, \quad Z(x,0) = Z_0(x) \geq 0, & x \in [0,\Omega], \end{cases} \tag{1.1}$$

in which $\Omega = [0, l\pi]$ $(l > 0)$; $P(x,t)$ and $Z(x,t)$ represent the phytoplankton and zooplankton population densities at time t and distance x, respectively; d_1 and d_2 are diffusion terms; r is the intrinsic growth rate of phytoplankton; K indicates the maximum capacity of phytoplankton environment; c and e are the maximum capture rate and conversion rate of zooplankton; μ is the natural mortality of zooplankton population; ρ indicates the toxin intensity; f is the proportion of phytoplankton that can be caught by zooplankton, therefore, the phytoplankton with ratio $1-f$ can aggregate to form a rough sphere, its surface area can be expressed as a function of $\rho P^{2/3}$.

In this paper, we introduce the habitat complexity effect into system (1.1). Comparing with the processing time h, the habitat complexity is more likely to affect the attack coefficient β, therefore, we use $\beta(1-m)$ to replace β, where m $(0 < m < 1)$ is a one-dimensional parameter used to measure the intensity of β. Assume that habitat complexity is homogeneous throughout the habitat, then the total amount of phytoplankton which is caught, $V(P)$, can be expressed as

$$\begin{cases} V(x) = \beta(1-m) T_s P, \\ T_s = T - hV(P), \end{cases}$$

where T_s is the available search time and T is the total time. By calculation, we have

$$V(P) = \frac{T\beta(1-m)P}{1+\beta(1-m)hP}.$$

Therefore, for system (1.1), the functional response function with habitat complexity effect is modified as

$$\frac{V(P)}{T} = \frac{\beta(1-m)P}{1+\beta h(1-m)P}.$$

Based on model (1.1), we introduce production delay, habitat complexity effect, and diffusion term to establish a toxic plankton model with Holling type II functional response function:

$$\begin{cases} \frac{\partial P(x,t)}{\partial t} = d_1 \Delta P + rP(1-\frac{P(t-\tau)}{K}) - \frac{c\beta(1-m)PZ}{1+h\beta(1-m)P}, & x \in \Omega, t > 0, \\ \frac{\partial Z(x,t)}{\partial t} = d_2 \Delta Z + \frac{e\beta(1-m)PZ}{1+h\beta(1-m)P} - \mu Z - e\rho P^{2/3} Z, & x \in \Omega, t > 0, \\ P_x(0,t) = P_x(\pi,t) = Z_x(0,t) = Z_x(\pi,t) = 0, & t \geq 0, \\ P(x,0) = P_0(x) \geq 0, \qquad Z(x,0) = Z_0(x) \geq 0, & x \in \Omega, \end{cases} \tag{1.2}$$

where $\Omega = [0, l\pi]$ $(l > 0)$.

The rest of this paper is organized into sections. In Sect. 2, by analyzing the roots of the characteristic equation, we discuss the stability of diffusion system without delay at the equilibria (including boundary equilibria and positive equilibrium). In Sect. 3, we study the existence of Hopf bifurcation for the delayed diffusion system and the bifurcation direction, and the stability of periodic solutions is discussed by employing the center manifold and normal form theory. In Sects. 4 and 5, a biological explanation is given and some numerical simulations are carried out.

2 Stability analysis of the system without delay

In order to ensure the biological significance of the system, we assume $c > e$. In the following, for system (1.2), we shall discuss the existence of its nonnegative equilibria. The equilibrium satisfies

$$\begin{cases} rP(1-\frac{P}{K}) - \frac{c\beta(1-m)PZ}{1+h\beta(1-m)P} = 0, \\ \frac{e\beta(1-m)PZ}{1+h\beta(1-m)P} - \mu Z - e\rho P^{2/3} Z = 0. \end{cases}$$

By calculation, system (2.1) has three equilibria $E_0 = (0,0)$, $E_1 = (K,0)$, and $E^* = (P^*, Z^*)$, where $Z^* = \frac{erP^*(1-\frac{P^*}{K})}{c\mu + ce\rho P^{*2/3}}$; $0 < P^* < K$ must hold to ensure that $Z^* > 0$. Let P^* be a root of $\frac{e\beta(1-m)P}{1+h\beta(1-m)P} - \mu - e\rho P^{2/3} = 0$, this implies P^* satisfies the following equation:

$$\begin{aligned} f(P) &= e^3\rho^3 h^3 \beta^3 (1-m)^3 P^5 + 3e^3\rho^3 h^2 \beta^2 (1-m)^2 P^4 \\ &\quad + \left[3e^3\rho^3 h\beta(1-m) - \beta^3(1-m)^3(e-\mu h)^3\right] P^3 \\ &\quad + \left[e^3\rho^3 + 3\mu\beta^2(1-m)^2(e-\mu h)^2\right] P^2 - 3\mu^2\beta(1-m)(e-\mu h)P + \mu^3. \end{aligned}$$

Obviously,

$$\begin{aligned} f'(P) &= 5e^3\rho^3 h^3 \beta^3 (1-m)^3 P^4 + 12e^3\rho^3 h^2 \beta^2 (1-m)^2 P^3 \\ &\quad + 3\left[3e^3\rho^3 h\beta(1-m) - \beta^3(1-m)^3(e-\mu h)^3\right] P^2 \\ &\quad + 2\left[e^3\rho^3 + 3\mu\beta^2(1-m)^2(e-\mu h)^2\right] P - 3\mu^2\beta(1-m)(e-\mu h). \end{aligned}$$

If $e-\mu h<0$, then $f'(P)>0$, $f(P)$ is monotone increasing on $[0,K]$, so $f(P)$ has no solution on $(0,K)$. If $e-\mu h>0$, then $f'(P)$ has at least one zero on $[0,K]$. We might as well assume $P_1\in[0,K]$ such that $f'(P_1)=0$. To make $P_1\in[0,K]$ be the minimum point of $f(P)=0$, we need $f''(P_1)>0$. We know

$$\begin{aligned} f''(P) &= 20e^3\rho^3h^3\beta^3(1-m)^3{P_1}^3+12e^3\rho^3h^2\beta^2(1-m)^2{P_1}^2 \\ &\quad +6\bigl[3e^3\rho^3h\beta(1-m)-\beta^3(1-m)^3(e-\mu h)^3\bigr]P_1 \\ &\quad +2\bigl[e^3\rho^3+3\mu\beta^2(1-m)^2(e-\mu h)^2\bigr], \end{aligned}$$

when $0<\beta<\frac{e\rho}{(1-m)(e-\mu h)}\sqrt{\frac{3e\rho h}{e-\mu h}}$, i.e., $m>1-\frac{e\rho}{\beta(e-\mu h)}\sqrt{\frac{3e\rho h}{e-\mu h}}$, $f''(P)>0$. Obviously, $f(P)$ has a positive root if $f(P_1)<0$. We make the following assumptions:

($\mathbf{H_0}$) $c>e$, $e-\mu h>0$,

($\mathbf{H_1}$) $f(P_1)<0$, $m>1-\frac{e\rho}{\beta(e-\mu h)}\sqrt{\frac{3e\rho h}{e-\mu h}}$.

Theorem 2.1 *If* ($\mathbf{H_0}$) *and* ($\mathbf{H_1}$) *hold, then system* (1.2) *has at least one positive equilibrium* $E^*=(P^*,Z^*)$.

2.1 Stability of positive equilibrium point

We assume that system (1.2) has only one positive equilibrium, denoted as $E^*=(P^*,Z^*)$. When $\tau=0$, we move $E^*=(P^*,Z^*)$ to $(0,0)$. Making a transformation $\bar{P}=P-P^*$, $\bar{Z}=Z-Z^*$, and omitting the bar, (1.2) becomes

$$\begin{cases} \frac{\partial P(x,t)}{\partial t}=d_1\Delta P+r(P+P^*)(1-\frac{P+P^*}{K})-\frac{c\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}, \\ \frac{\partial Z(x,t)}{\partial t}=d_2\Delta Z+\frac{e\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}-\mu(Z+Z^*)-e\rho(P+P^*)^{2/3}(Z+Z^*). \end{cases} \tag{2.1}$$

Defining the real Sobolev space

$$X:=\bigl\{(P,Z)^T\bigm|P,Z\in H^2(0,l\pi),(P_x,Z_x)\bigr|_{x=0,l\pi}=(0,0)\bigr\},$$

the complexification of X is

$$X_c:=X\oplus iX=\{x_1+ix_2|x_1,x_2\in X\}.$$

Let $U=(P,Z)\in H^2(0,l\pi)$, $D=\operatorname{diag}(d_1,d_2)$, then system (2.1) can be written as an abstract functional differential equation

$$\dot{U}(t)=D\Delta U(t)+L(m)U(t)+F\bigl(U(t)\bigr),$$

where

$$\begin{aligned} L(m) &= \begin{pmatrix} a_1(m) & a_2(m) \\ a_3(m) & 0 \end{pmatrix}, \\ F\bigl(U(t)\bigr) &= \begin{pmatrix} r(P+P^*)(1-\frac{P+P^*}{K})-\frac{c\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}-a_1(m)P-a_2(m)Z \\ \frac{e\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}-\mu(Z+Z^*)-e\rho(P+P^*)^{2/3}(Z+Z^*)-a_3(m)P \end{pmatrix}. \end{aligned}$$

For system (2.1), the linearized equation at $(m,0,0)$ is

$$\dot{U}(t) = D\Delta U(t) + L(m)U(t),$$

where

$$L(m) = D\frac{\partial^2}{\partial x^2} + J(F)\Big|_{U\equiv 0} = \begin{pmatrix} a_1(m) + d_1\frac{\partial^2}{\partial x^2} & a_2(m) \\ a_3(m) & d_2\frac{\partial^2}{\partial x^2} \end{pmatrix}.$$

We use $\mu_n = \frac{n^2}{l^2}$ $(n = 0,1,2,\dots)$ to represent the nth eigenvalue of $-\varphi_{xx} = \mu\varphi$, $\varphi_x|_{x=0,l\pi} = 0$. Define the linear operator

$$L_n(m) = \begin{pmatrix} a_1(m) - d_1\mu_n & a_2(m) \\ a_3(m) & -d_2\mu_n \end{pmatrix},$$

in which

$$\begin{aligned} a_1(m) &= r - \frac{2rP^*}{K} - \frac{r(1-\frac{P^*}{K})}{1+h\beta(1-m)P^*}, \\ a_2(m) &= -\frac{c}{e}\bigl(\mu + e\rho P^{*2/3}\bigr) < 0, \\ a_3(m) &= \left(\frac{\mu + e\rho P^{*2/3}}{1+h\beta(1-m)P^*} - \frac{2}{3}e\rho P^{*-1/3}\right)Z^*. \end{aligned}$$

It is easy to obtain that the eigenvalue of $L(m)$ can be given by the eigenvalue of $L_n(m)$, and the eigenequation of $L_n(m)$ is

$$\lambda^2 + T_n(m)\lambda + D_n(m) = 0, \tag{2.2}$$

in which

$$\begin{aligned} T_n(m) &= -\operatorname{tr}\bigl(L_n(m)\bigr) = -a_1(m) + (d_1+d_2)\mu_n \\ &= -r + \frac{2rP^*}{K} + \frac{r(1-\frac{P^*}{K})}{1+h\beta(1-m)P^*} + (d_1+d_2)\mu_n, \\ D_n(m) &= \bigl|L_n(m)\bigr| = d_1d_2{\mu_n}^2 - a_1(m)d_2\mu_n - a_2(m)a_3(m) \\ &= d_1d_2{\mu_n}^2 - \left(r - \frac{2rP^*}{K} - \frac{r(1-\frac{P^*}{K})}{1+h\beta(1-m)P^*}\right)d_2\mu_n \\ &\quad + \left(\frac{\mu + e\rho P^{*2/3}}{1+h\beta(1-m)P^*} - \frac{2}{3}e\rho P^{*-1/3}\right)rP^*\left(1 - \frac{P^*}{K}\right). \end{aligned}$$

The characteristic roots of (2.2) are

$$\lambda_{1,2}^{(n)}(m) = \frac{-T_n(m) \pm \sqrt{{T_n}^2(m) - 4D_n(m)}}{2}, \quad n \in \mathbb{N}_0 \triangleq \{0\} \cup \mathbb{N}.$$

Theorem 2.2 *Assume* $(\mathbf{H_0})$ *and* $(\mathbf{H_1})$ *hold and* $\frac{K}{2} < P^* < K$. *Then the following conclusions are true*:

(1) *If* $m > 1 - \frac{1}{h\beta P^*}(\frac{\mu+e\rho P^{*2/3}}{2/3e\rho P^{*-1/3}} - 1)$, *then* $T_n(m) > 0$, $D_n(m) > 0$, *the roots of Eq.* (2.1) *have negative real parts, and system* (2.1) *is locally asymptotically stable at* $E^* = (P^*, Z^*)$;

(2) *If* $m \le 1 - \frac{1}{h\beta P^*}(\frac{\mu+e\rho P^{*2/3}}{2/3e\rho P^{*-1/3}} - 1)$, *then* $D_0(m) < 0$, *Eq.* (2.1) *has at least one root with positive real part, and system* (2.1) *is unstable at* $E^* = (P^*, Z^*)$.

Theorem 2.3 *Assume* $(\mathbf{H_0})$ *and* $(\mathbf{H_1})$ *hold and* $0 < P^* < \frac{K}{2}$. *Then the following conclusions are true*:

(1) *If* $m > \max\{1 - \frac{1}{h\beta P^*}(\frac{\mu+e\rho P^{*2/3}}{2/3e\rho P^{*-1/3}} - 1), 1 - \frac{1}{h\beta(K-2P^*)}\}$, *then* $T_n(m) > 0$, $D_n(m) > 0$, *the roots of Eq.* (2.1) *have negative real parts, and system* (2.1) *is locally asymptotically stable at* $E^* = (P^*, Z^*)$;

(2) *If* $m \le 1 - \frac{1}{h\beta(K-2P^*)}$ *or* $m \le 1 - \frac{1}{h\beta P^*}(\frac{\mu+e\rho P^{*2/3}}{2/3e\rho P^{*-1/3}} - 1)$, *then* $T_0(m) < 0$, *Eq.* (2.1) *has at least one root with positive real part, and system* (2.1) *is unstable at* $E^* = (P^*, Z^*)$.

2.2 Stability of boundary equilibrium points

Linearizing system (2.1) at the equilibrium, the corresponding characteristic roots at $E_0 = (0, 0)$ are

$$\lambda_{01}^n = r - d_1{\mu_n}^2, \qquad \lambda_{02}^n = -\mu - d_2{\mu_n}^2 < 0, \quad n \in \mathbb{N}_0,$$

the corresponding characteristic roots at $E_1 = (K, 0)$ are

$$\lambda_{11}^n = -r - d_1{\mu_n}^2 < 0, \qquad \lambda_{12}^n = \frac{e\beta(1-m)K}{1 + h\beta(1-m)K} - \mu - e\rho K^{2/3} - d_2{\mu_n}^2, \quad n \in \mathbb{N}_0.$$

Theorem 2.4 *For system* (2.1), *we have the following conclusions*:

(1) *The system is unstable at* $E_0 = (0, 0)$;

(2) *If* $m > 1 - \frac{\mu+e\rho K^{2/3}}{\beta K[e-h(\mu+e\rho K^{2/3})]}$, *then* $E_1 = (K, 0)$ *is locally asymptotically stable*; *if* $m < 1 - \frac{\mu+e\rho K^{2/3}}{\beta K[e-h(\mu+e\rho K^{2/3})]}$, *then* $E_1 = (K, 0)$ *is unstable.*

3 Stability and bifurcation analysis of the delayed system

In nature, the change of population size is not only related to the current state, but also depends on the previous state. Considering the influence of the past state on the population size, we take the time delay as a bifurcation parameter to study the delay effect on the dynamic properties of the system, including the stability of positive equilibrium, the existence and direction of Hopf bifurcation, and the stability of bifurcating periodic solutions.

3.1 Stability switch and existence of Hopf bifurcation

Assuming that system (2.1) has a unique positive equilibrium $E^* = (P^*, Z^*)$, we move it to $(0, 0)$ and make a transformation $\hat{P} = P - P^*$, $\hat{Z} = Z - Z^*$. In order to research conveniently, we still use P, Z to denote $\hat{P}$, $\hat{Z}$, respectively. Then system (2.1) becomes

$$\begin{cases} \frac{\partial P(x,t)}{\partial t} = d_1\Delta P + r(P + P^*)(1 - \frac{P(t-\tau)+P^*}{K}) - \frac{c\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}, \\ \frac{\partial Z(x,t)}{\partial t} = d_2\Delta Z + \frac{e\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)} - \mu(Z + Z^*) - e\rho(P + P^*)^{2/3}(Z + Z^*). \end{cases} \tag{3.1}$$

Letting

$$u_1(t) = P(\cdot, t), \qquad u_2(t) = Z(\cdot, t), \qquad U = (u_1, u_2)^T, \qquad X = C\big([0, l\pi], R^2\big),$$

system (3.1) can be written as an abstract differential equation in the phase space $\mathbb{C}_\tau = C([-\tau,0],X)$, namely

$$\dot{U}(t) = D\Delta U(t) + L(U_t) + F(U_t), \tag{3.2}$$

in which $D = \begin{pmatrix} d_1 & \\ & d_2 \end{pmatrix}$, $L : \mathbb{C}_\tau \to X$, $F : \mathbb{C}_\tau \to X$ are defined as follows: for $\phi = (\phi_1, \phi_2)^T$,

$$L(\phi) = \begin{pmatrix} a_1 & a_2 \\ a_3 & 0 \end{pmatrix}\begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + \begin{pmatrix} b_1 & 0 \\ 0 & 0 \end{pmatrix}\begin{pmatrix} \phi_1(-\tau) \\ \phi_2(-\tau) \end{pmatrix}, \qquad F(\phi) = \begin{pmatrix} F_1(\phi) \\ F_2(\phi) \end{pmatrix},$$

with

$$\begin{aligned}
F_1(\phi) &= r\big(\phi_1(0) + P^*\big)\left(1 - \frac{\phi_1(-\tau) + P^*}{K}\right) - \frac{c\beta(1-m)(\phi_1(0)+P^*)(\phi_2(0)+Z^*)}{1 + h\beta(1-m)(\phi_1(0)+P^*)} \\
&\quad - a_1\phi_1(0) - a_2\phi_2(0) - b_1\phi_1(-\tau), \\
F_2(\phi) &= \frac{e\beta(1-m)(\phi_1(0)+P^*)(\phi_2(0)+Z^*)}{1 + h\beta(1-m)(\phi_1(0)+P^*)} - \mu\big(\phi_2(0) + Z^*\big) \\
&\quad - e\rho\big(\phi_1(0) + P^*\big)^{2/3}\big(\phi_2(0) + Z^*\big) - a_3\phi_1(0), \\
a_1 &= r\left(1 - \frac{P^*}{K}\right) - \frac{c\beta(1-m)Z^*}{[1 + h\beta(1-m)P^*]^2}, \qquad a_2 = -\frac{c}{e}\big(\mu + e\rho P^{*2/3}\big) < 0, \\
a_3 &= \frac{e\beta(1-m)Z^*}{[1 + h\beta(1-m)P^*]^2} - \frac{2}{3}e\rho P^{*-1/3}Z^*, \qquad b_1 = -\frac{r}{K}P^* < 0.
\end{aligned}$$

Then, the linearized equation of (3.2) at $(0,0)$ is

$$\dot{U}(t) = D\Delta U(t) + L(U_t), \tag{3.3}$$

in which

$$L(U_t) = L_1U + L_2U_t, \qquad L_1 = \begin{pmatrix} a_1 & a_2 \\ a_3 & 0 \end{pmatrix}, \qquad L_2 = \begin{pmatrix} b_1 & 0 \\ 0 & 0 \end{pmatrix}.$$

For $-\varphi'' = \mu\varphi$, $x \in (0, l\pi)$, $\varphi'(0) = \varphi'(l\pi) = 0$, denote $\{b_n\}_{n=0}^{\infty}$ as the eigenvectors of the eigenvalues $\mu_n = n^2/l^2$, $n \in \mathbb{N}_0$, where $b_n = \cos\frac{n\pi}{l}$. Substitute $y = \sum_{n=0}^{\infty}\begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix}\cos\frac{n\pi}{l}$ into Eq. (3.3), we can obtain

$$\begin{pmatrix} a_1 + b_1e^{-\lambda\tau} - d_1\mu_n & a_2 \\ a_3 & -d_2\mu_n \end{pmatrix}\begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix} = \lambda\begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix}, \quad n \in \mathbb{N}_0.$$

The corresponding characteristic equation is

$$\det\big(\lambda I + \mu_nD - L_1 - L_2e^{-\lambda\tau}\big) = 0, \quad n \in \mathbb{N}_0.$$

Thus the characteristic equation is equivalent to

$$f_n(\lambda, \tau) = \lambda^2 + A_n\lambda + B_n + C_ne^{-\lambda\tau} = 0, \tag{3.4}$$

with

$$A_n = (d_1 + d_2)\mu_n - a_1, \qquad B_n = d_1 d_2 {\mu_n}^2 - a_1 d_2 \mu_n - a_2 a_3, \qquad C_n = -b_1(\lambda + d_2 \mu_n).$$

We make the following hypotheses:

($\mathbf{H_2}$) $a_1 < 0$,

($\mathbf{H_3}$) $b_1 < a_1$,

($\mathbf{H_4}$) ${a_1}^2 + 2a_2 a_3 - {b_1}^2 > 0$.

Lemma 3.1 *If* ($\mathbf{H_0}$)–($\mathbf{H_2}$) *hold, for* $n \in \mathbb{N}_0$, *then the following conclusions can be drawn*:

(1) *When* $\tau = 0$, *all the characteristic roots of Eq.* (3.4) *have negative real parts and system* (3.1) *is locally asymptotically stable at* $E^* = (P^*, Z^*)$;

(2) $\lambda = 0$ *is not the root of Eq.* (3.4).

Lemma 3.2 *Assuming* ($\mathbf{H_0}$)–($\mathbf{H_2}$) *are true, when* $\tau \neq 0$, *we have the following conclusions*:

(1) *If* ($\mathbf{H_3}$) *holds, when* $N_1 \leq n \leq \min\{N_2, N_3\}$, *Eq.* (3.4) *has a pair of pure imaginary roots* $\pm i\omega_n^+$ *at* $\tau = \tau_n^{j,+}$;

(2) *If* ($\mathbf{H_3}$) *holds, when* $\max\{N_1, N_3\} < n < N_2$, *Eq.* (3.4) *has a pair of pure imaginary roots* $\pm i\omega_n^+$ *at* $\tau = \tau_n^{j,+}$;

(3) *If* ($\mathbf{H_3}$) *holds, when* $0 \leq n \leq \min\{N_1, N_3\}$ *or* $N_2 < n < N_3$, *Eq.* (3.4) *has two pairs of pure imaginary roots* $\pm i\omega_n^{\pm}$ *at* $\tau = \tau_n^{j,\pm}$;

(4) *If* ($\mathbf{H_3}$) *holds, when* $n > \max\{N_2, N_3\}$ *or* $N_3 < n < N_1$, *Eq.* (3.4) *has no pure imaginary root*;

(5) *If* ($\mathbf{H_4}$) *holds, when* $n \geq 0$, *Eq.* (3.4) *has no pure imaginary root, where*

$$N_1 = \begin{cases} [\hat{N} = l\sqrt{\frac{1}{2d_1 d_2}[(a_1 - b_1)d_2 - \sqrt{((a_1 - b_1)d_2)^2 + 4d_1 d_2 a_2 a_3}]}], & \hat{N} \notin \mathbb{N}, \\ [\hat{N} = l\sqrt{\frac{1}{2d_1 d_2}[(a_1 - b_1)d_2 - \sqrt{((a_1 - b_1)d_2)^2 + 4d_1 d_2 a_2 a_3}]}] - 1, & \hat{N} \in \mathbb{N}, \end{cases}$$

$$N_2 = \begin{cases} [\hat{N} = l\sqrt{\frac{1}{2d_1 d_2}[(a_1 - b_1)d_2 + \sqrt{((a_1 - b_1)d_2)^2 + 4d_1 d_2 a_2 a_3}]}], & \hat{N} \notin \mathbb{N}, \\ [\hat{N} = l\sqrt{\frac{1}{2d_1 d_2}[(a_1 - b_1)d_2 + \sqrt{((a_1 - b_1)d_2)^2 + 4d_1 d_2 a_2 a_3}]}] - 1, & \hat{N} \in \mathbb{N}, \end{cases}$$

$$N_3 = \begin{cases} [\tilde{N} = l\sqrt{\frac{1}{(d_1^2 + d_2^2)}[a_1 d_1 + \sqrt{d_1^2 {a_1}^2 - (d_1^2 + d_2^2)({a_1}^2 + 2a_2 a_3 - {b_1}^2)}]}], & \tilde{N} \notin \mathbb{N}, \\ [\tilde{N} = l\sqrt{\frac{1}{(d_1^2 + d_2^2)}[a_1 d_1 + \sqrt{d_1^2 {a_1}^2 - (d_1^2 + d_2^2)({a_1}^2 + 2a_2 a_3 - {b_1}^2)}]}] \\ \quad - 1, & \tilde{N} \in \mathbb{N}, \end{cases}$$

$$\tau_n^{j,\pm} = \frac{1}{\omega_n^{\pm}} \arccos \frac{(D_n + c_1 A_n)(\omega_n^{\pm})^2 - D_n B_n}{{D_n}^2 + {c_1}^2(\omega_n^{\pm})^2} + \frac{2j\pi}{\omega_n^{\pm}}, \quad j \in \mathbb{N}_0.$$

Proof We seek the critical value τ such that Eq. (3.4) has a pair of pure imaginary roots. Let $\lambda = i\omega$ ($\omega > 0$) be the root of Eq. (3.4), for some $n \in \mathbb{N}_0$, then ω satisfies

$$-\omega^2 + i\omega A_n + B_n + b_1(i\omega + d_2\mu_n)(\cos\omega\tau - i\sin\omega\tau) = 0.$$

Separating the real and imaginary parts, we have

$$\begin{cases} b_1\omega\sin\omega\tau + b_1 d_2\mu_n\cos\omega\tau = \omega^2 - B_n, \\ b_1 d_2\mu_n\sin\omega\tau - b_1\omega\cos\omega\tau = A_n\omega. \end{cases} \tag{3.5}$$

Denoting $D_n = b_1 d_2\mu_n$, we get

$$\omega^4 + \left({A_n}^2 - 2B_n - {b_1}^2\right)\omega^2 + {B_n}^2 - {D_n}^2 = 0. \tag{3.6}$$

Let $z = \omega^2$, then (3.6) becomes

$$z^2 + \left({A_n}^2 - 2B_n - {b_1}^2\right)z + {B_n}^2 - {D_n}^2 = 0. \tag{3.7}$$

If $(\mathbf{H_3})$ holds, obviously, $B_n - D_n = d_1 d_2 {\mu_n}^2 - (b_1 + a_1)d_2\mu_n - a_2 a_3 > 0$. Next, we discuss the symbol of $B_n + D_n$. We know $B_n + D_n = d_1 d_2{\mu_n}^2 + (b_1 - a_1)d_2\mu_n - a_2a_3$. If $N_1 \le n \le N_2$, $B_n + C_n < 0$, then ${B_n}^2 - {C_n}^2 < 0$. If $n > N_2$ or $0 < n \le N_1$, $B_n + C_n > 0$, then ${B_n}^2 - {C_n}^2 > 0$. Similarly, ${A_n}^2 - 2B_n - {b_1}^2 = ({d_1}^2 + {d_2}^2){\mu_n}^2 - 2a_1d_1\mu_n + {a_1}^2 + 2a_2a_3 - {b_1}^2$; ${A_n}^2 - 2B_n - {b_1}^2 < 0$ for $0 \le n \le N_3$ and ${A_n}^2 - 2B_n - {b_1}^2 \ge 0$ for $n > N_3$.

Under $(\mathbf{H_4})$, ${A_n}^2 - 2B_n - {b_1}^2 = ({d_1}^2 + {d_2}^2){\mu_n}^2 - 2a_1d_1\mu_n + {a_1}^2 + 2a_2a_3 - {b_1}^2$ monotonically increases with respect to n, therefore, for any $n \ge 0$, ${A_n}^2 - 2B_n - {b_1}^2 > 0$, and $B_n + D_n = d_1d_2{\mu_n}^2 + (b_1 - a_1)d_2\mu_n - a_2a_3 > 0$, so ${B_n}^2 - {D_n}^2 > 0$.

In summary, the conclusions are true, and the roots of Eq. (3.7) are

$$z_n^{\pm} = \frac{-({A_n}^2 - 2B_n - {b_1}^2) \pm \sqrt{({A_n}^2 - 2B_n - {b_1}^2)^2 - 4({B_n}^2 - {D_n}^2)}}{2}.$$

Equation (3.6) has at least one positive root $z_n^{\pm}$, $\omega_n^{\pm} = \sqrt{z_n^{\pm}}$. □

Lemma 3.3 *Suppose* $(\mathbf{H_3})$ *is true, then the transversality conditions hold,* $\alpha'(\tau_n^{j,+}) = \frac{d\lambda}{d\tau}|_{\tau=\tau_n^{j,+}} > 0$, $\alpha'(\tau_n^{j,-}) = \frac{d\lambda}{d\tau}|_{\tau=\tau_n^{j,-}} < 0$.

Proof Differentiating $\lambda^2 + A_n\lambda + B_n + ce^{-\lambda\tau}(\lambda + C_n) = 0$ with respect to τ, we have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + A_n)e^{\lambda\tau} + c}{c\lambda(\lambda + C_n)} - \frac{\tau}{\lambda}.$$

As

$$\operatorname{sign}\left\{\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)\right\}_{\lambda=i\omega_n^{\pm}} = \operatorname{sign}\left\{\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\omega_n^{\pm}},$$

we obtain

$$\begin{aligned}\operatorname{sign}\left\{\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)\right\}_{\lambda=i\omega_n^{\pm}} &= \operatorname{sign}\left\{\operatorname{Re}\left(\frac{(2\lambda+A_n)e^{\lambda\tau}+c}{c\lambda(\lambda+C_n)}-\frac{\tau}{\lambda}\right)\right\}_{\lambda=i\omega_n^{\pm}} \\ &= \operatorname{sign}\left\{\frac{2\omega^2-2B_n+{A_n}^2-c^2}{c^2(\omega^2+C_n^2)}\right\} \\ &= \operatorname{sign}\left\{\frac{\pm\sqrt{({A_n}^2-2B_n-c^2)^2-4({B_n}^2-c^2{C_n}^2)}}{c^2(\omega^2+C_n^2)}\right\}.\end{aligned}$$

So $\alpha'(\tau_n^{j,+})=\frac{d\lambda}{d\tau}|_{\tau=\tau_n^{j,+}}>0$, $\alpha'(\tau_n^{j,-})=\frac{d\lambda}{d\tau}|_{\tau=\tau_n^{j,-}}<0$. □

Theorem 3.1 *Under* $(\mathbf{H_0})$–$(\mathbf{H_2})$, *if also* $(\mathbf{H_3})$ *and* $(\mathbf{H_4})$ *are true, then for system* (3.1), *we can derive the following conclusions*:

(1) *If* $\tau_1^{0,-}>\tau_1^{1,+}$, *then* $E^*=(P^*,Z^*)$ *is locally asymptotically stable for* $\tau\in[0,\tau_1^{0,+})$, *and* $E^*=(P^*,Z^*)$ *is unstable for* $\tau\in(\tau_1^{0,+},+\infty)$. *A family of nonhomogeneous bifurcating periodic solutions occur nearby* $\tau=\tau_1^{j,\pm}$, $j\in\mathbb{N}_0$;

(2) *If* $\tau_1^{0,-}<\tau_1^{1,+}$, *then there exists a positive integer* k *such that* $E^*=(P^*,Z^*)$ *switches* k *times from stable to unstable, then from unstable to stable, finally becoming unstable, i.e., when*

$$\tau\in\left[0,\tau_1^{0,+}\right)\cup\left(\tau_1^{0,-},\tau_1^{1,+}\right)\cup\cdots\cup\left(\tau_1^{k-1,-},\tau_1^{k,+}\right),$$

$E^*=(P^*,Z^*)$ *is locally asymptotically stable*; *when*

$$\tau\in\left(\tau_1^{0,+},\tau_1^{0,-}\right)\cup\left(\tau_1^{1,+},\tau_1^{1,-}\right)\cup\cdots\cup\left(\tau_1^{k-1,+},\tau_1^{k-1,-}\right)\cup\left(\tau_1^{k,+},+\infty\right),$$

$E^*=(P^*,Z^*)$ *is unstable*;

(3) *When* $\tau=\tau_1^{j,\pm}$, $j\in\mathbb{N}_0$, *a Hopf bifurcation occurs at* $E^*=(P^*,Z^*)$, *and the bifurcating periodic solutions are homogeneous*; *when* $\tau\in\{\tau_n^{j,\pm}:\tau_n^{j,\pm}\neq\tau_m^{i,\pm},m\neq n,N_2<n<N_3,j,i\in\mathbb{N}_0\}/\{\tau_1^{j,\pm}|k\in\mathbb{N}_0\}$, *the system also undergoes a Hopf bifurcation at* $E^*=(P^*,Z^*)$, *and the bifurcating periodic solutions are nonhomogeneous*.

3.2 Property analysis of Hopf bifurcation

In this section, we use the theory of normal form and center manifold theorem to discuss the direction of Hopf bifurcation and the stability of bifurcating periodic solutions. Let $\bar{P}(x,t)=P(x,\tau t)-P^*$, $\bar{Z}(x,t)=Z(x,\tau t)-Z^*$; for convenience, we remove the horizontal line and use $\bar{\tau}$ to represent the critical value $\tau_n^{j,\pm}$. Then system (2.1) can be written as

$$\begin{cases}\frac{\partial P(x,t)}{\partial t}=d_1\Delta P+\bar{\tau}[r(P+P^*)(1-\frac{P(t-1)+P^*}{K})-\frac{c\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}],\\ \frac{\partial Z(x,t)}{\partial t}=d_2\Delta Z\\ \qquad+\bar{\tau}[\frac{e\beta(1-m)(P+P^*)(Z+Z^*)}{1+h\beta(1-m)(P+P^*)}-\mu(Z+Z^*)-e\rho(P+P^*)^{2/3}(Z+Z^*)].\end{cases}\tag{3.8}$$

Let $\tau=\bar{\tau}+\sigma$, $u_1(t)=P(\cdot,t)$, $u_2(t)=Z(\cdot,t)$, $U=(u_1,u_2)^T$, then in the phase space $\ell_1:=C([-1,0],X)$, system (3.8) can be written in abstract form as

$$\frac{dU(t)}{dt}=\bar{\tau}D\Delta U(t)+L_{\bar{\tau}}(U_t)+F(U_t,\sigma),\tag{3.9}$$

where $L_\sigma(\phi)$ and $F(\phi,\sigma)$ are defined by

$$L_\sigma(\phi) = \sigma L_1 \begin{pmatrix}\phi_1(0)\\ \phi_2(0)\end{pmatrix} + \sigma L_2 \begin{pmatrix}\phi_1(-1)\\ \phi_2(-1)\end{pmatrix} = \sigma \begin{pmatrix} a_1\phi_1(0) + a_2\phi_2(0) + b_1\phi_1(-1) \\ a_3\phi_1(0)\end{pmatrix}, \tag{3.10}$$

$$F(\phi,\sigma) = \sigma D\Delta\phi + L_\sigma(\phi) + f(\phi,\sigma), \qquad f(\phi,\sigma) = (\bar\tau + \sigma)\big(F_1(\phi,\sigma),F_2(\phi,\sigma)\big)^T, \tag{3.11}$$

with

$$\begin{aligned}
&\phi = (\phi_1,\phi_1)^T \in \ell_1,\\
&F_1(\phi) = \big(\phi_1(0)+P_0\big)\big(1-\big(\phi_1(0)+P_0\big)\big) - \frac{(\phi_1(0)+P_0)(\phi_2(-1)+Z_0)}{\alpha + (\phi_1(0)+P_0)} e^{-(\phi_1(0)+P_0)}\\
&\qquad - a_1\phi_1(0) - a_2\phi_2(0) - b_1\phi_1(-1),\\
&F_2(\phi) = \frac{e\beta(1-m)(\phi_1(0)+P^*)(\phi_2(0)+Z^*)}{1+h\beta(1-m)(\phi_1(0)+P^*)} - \mu\big(\phi_2(0)+Z^*\big)\\
&\qquad - e\rho\big(\phi_1(0)+P^*\big)^{2/3}\big(\phi_2(0)+Z^*\big) - a_3\phi_1(0),
\end{aligned}$$

as well as

$$\begin{aligned}
&L_\sigma(U_t) = L_1U + L_2U_t, \qquad L_1 = \begin{pmatrix} a_1 & a_2\\ a_3 & 0\end{pmatrix}, \qquad L_2 = \begin{pmatrix} b_1 & 0\\ 0 & 0\end{pmatrix}, \qquad U = (P,Z)^T,\\
&U_t = (P_t,Z_t)^T, \qquad a_1 = f_p = r\left(1-\frac{P^*}{K}\right) - \frac{c\beta(1-m)Z^*}{[1+h\beta(1-m)P^*]^2},\\
&a_2 = f_z = -\frac{c\beta(1-m)P^*}{1+h\beta(1-m)P^*} < 0, \qquad b_1 = f_{p_t} = -\frac{r}{K}P^* < 0,\\
&a_3 = g_p = \frac{e\beta(1-m)Z^*}{[1+h\beta(1-m)P^*]^2} - \frac{2}{3}e\rho P^{*-1/3}Z^*.
\end{aligned}$$

Obviously, $(0,0)$ is the equilibrium of Eq. (3.8), its linearized equation is

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = \bar\tau D\Delta U(t) + L_\sigma(U_t), \tag{3.12}$$

in which $\Lambda_n = \{i\omega_n\bar\tau, -i\omega_n\bar\tau\}$ are the characteristic roots of system (3.12) satisfying $\frac{dz(t)}{dt} = -\bar\tau d\frac{n^2}{l^2}z(t) + L_{\bar\tau}(z_t)$. By Riesz representation, there exists a matrix whose components are bounded variation functions $\eta_n(\sigma,\theta)$, $\theta \in [-1,0]$ such that

$$-(\bar\tau + \sigma_n)D\phi(0) + L_{\sigma_n}(\phi) = \int_{-1}^0 \mathrm{d}\eta_n(\sigma,\theta)\phi(\theta).$$

In fact, we can choose $\eta_n(\sigma,\theta) = \bar\tau[L_1\delta(\theta) + L_2\delta(\theta+1)]$, where $\delta(\theta)$ is the Dirac delta function. Let A be the infinitesimal generating function corresponding to (3.12), and A^* be the adjoint matrix of A under the bilinear paring

$$\begin{aligned}
\big\langle\psi(s),\phi(\theta)\big\rangle &= \bar\psi(0)\phi(0) - \int_{-1}^0\int_{\varsigma=0}^{\theta} \bar\psi(\varsigma-\theta)\,\mathrm{d}\zeta_n(\theta)\phi(\varsigma)\,\mathrm{d}\varsigma\\
&= \bar\psi(0)\phi(0) + \bar\tau\int_{-1}^0 \bar\psi(\varsigma+1)K_2\phi(\varsigma)\,\mathrm{d}\varsigma,
\end{aligned} \tag{3.13}$$

with $\phi \in C^1([-1,0],R^2)$, $\psi \in C^1([-1,0],R^2)$, $\zeta_n(\theta) = \zeta(\theta,0)$. Denote $p(\boldsymbol{\theta}) = (1,\xi)^T e^{i\omega_n\bar{\tau}\theta}$, $p^*(\boldsymbol{\theta}) = \Gamma(\eta,1)^T e^{i\omega_n\bar{\tau}\theta}$ as the eigenvectors of operators A and A^* corresponding to the eigenvalues $i\omega_n\bar{\tau}$ and $-i\omega_n\bar{\tau}$. Then

$$\eta = \frac{-i\omega_n + d_2\mu_n}{a_2}, \qquad \xi = \frac{a_3}{d_2\mu_n + i\omega_n}, \qquad \Gamma = \left(\bar{\xi} + \eta + \eta b_1 e^{-i\omega_n\bar{\tau}}\right)^{-1}.$$

Decompose the space ℓ_1 into the direct sum of the generalized eigenspace P and its supplementary space Q, where

$$P := \{zpb_n + \bar{z}\bar{p}b_n \mid z \in \mathbb{C}\}, \qquad Q := \left\{\phi \in \mathcal{C} \mid \left(\bar{p}^* b_n, \phi\right) = 0, \left(p^* b_n, \phi\right) = 0\right\}.$$

Therefore, the solution of abstract differential equation (3.2) can be decomposed as

$$\begin{pmatrix} p_t \\ z_t \end{pmatrix} = z(t)p(\theta)b_n + \bar{z}(t)\bar{p}(\theta)b_n + W(t,\theta). \tag{3.14}$$

Denote $z(t) = (p^* b_n, p_t)|b_n|^{-2}$, $W(t,\theta) = p_t(\theta) - 2\operatorname{Re}\{z(t)p(\theta)b_n\}$, there exists a central manifold $\mathcal{C}_0$ on which there is

$$\begin{aligned} W(t,\theta) &= W_{20}\frac{z^2}{2} + W_{11}z\bar{z} + W_{02}\frac{\bar{z}^2}{2} + \cdots \\ &= \begin{pmatrix} W_{20}^{(1)} \\ W_{20}^{(2)} \end{pmatrix}\frac{z^2}{2} + \begin{pmatrix} W_{11}^{(1)} \\ W_{11}^{(2)} \end{pmatrix} z\bar{z} + \begin{pmatrix} W_{02}^{(1)} \\ W_{02}^{(2)} \end{pmatrix}\frac{\bar{z}^2}{2} + \cdots, \end{aligned} \tag{3.15}$$

in which z and $\bar{z}$ are the local coordinates corresponding to pb_n and $\bar{p}b_n$, respectively. When $p_t \in \mathcal{C}_0$, we represent the nonlinear term $F(\alpha_0, u_t)$ as $F(\alpha_0, u_t)|_{\mathcal{C}_0} = \tilde{F}(\alpha_0, z, \bar{z})$. Denote

$$g(z,\bar{z}) = \bar{p}^{*T}(0)\left\langle \tilde{F}(\alpha_0, z, \bar{z}), \beta_n \right\rangle = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots, \tag{3.16}$$

on the central manifold $\mathcal{C}_0$,

$$z(t) = i\omega_n z(t) + \bar{p}^T(0)\begin{pmatrix} \langle F_1, b_n\rangle \\ \langle F_2, b_n\rangle \end{pmatrix} = i\omega_n z(t) + g(z,\bar{z}). \tag{3.17}$$

By comparing coefficients, we derive

$$\begin{aligned} g_{20} &= \bar{\Gamma}\left[\bar{\eta}\left(f_{pp} + 2f_{pz}a + 2f_{pp_t}e^{-i\omega_n\bar{\tau}}\right) + g_{pp} + 2g_{pz}a\right], \\ g_{11} &= \bar{\Gamma}\left\{\bar{\eta}\left[f_{pp} + f_{pz}(a+\bar{a}) + f_{pp_t}\left(e^{i\omega_n\bar{\tau}} + e^{-i\omega_n\bar{\tau}}\right)\right] + g_{pp} + g_{pz}(a+\bar{a})\right\}, \\ g_{02} &= \bar{g}_{20}, \\ g_{21} &= \frac{3}{8}\bar{\Gamma}(\bar{\eta}T_1 + T_2) + \bar{\Gamma}\left(\bar{\eta}\int_\Omega T_3 b_k^2\,\mathrm{d}x + \int_\Omega T_4 b_k^2\,\mathrm{d}x\right), \end{aligned}$$

where

$$T_1 = f_{ppp} + f_{ppz}(2a+\bar{a}), T_2 = g_{ppp} + f_{ppz}(2a+\bar{a}),$$

$$\begin{aligned}
T_3 ={}& f_{pp}\left(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)\right) \\
&+ 2f_{pz}\left(\frac{1}{2}W_{20}^{(2)}(0) + \frac{\bar{a}}{2}W_{20}^{(1)}(0) + aW_{11}^{(1)}(0) + W_{11}^{(2)}(0)\right) \\
&+ 2f_{pp_t}\left(\frac{1}{2}W_{20}^{(1)}(-1) + \frac{1}{2}W_{20}^{(1)}(0)e^{i\omega_n\bar{\tau}} + W_{11}^{(1)}(-1) + W_{11}^{(1)}(0)e^{-i\omega_n\bar{\tau}}\right), \\
T_4 ={}& g_{pp}\left(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)\right) \\
&+ 2g_{pz}\left(\frac{1}{2}W_{20}^{(2)}(0) + \frac{\bar{a}}{2}W_{20}^{(1)}(0) + aW_{11}^{(1)}(0) + W_{11}^{(2)}(0)\right),
\end{aligned}$$

with

$$\begin{aligned}
f_{pp} &= 2ch\beta^2(1-m)^2\left[1 + h\beta(1-m)P^*\right]^{-3}Z^*, \qquad f_{pp_t} = -\frac{r}{K}, \\
f_{pz} &= -c\beta(1-m)\left[1 + h\beta(1-m)P^*\right]^{-2}, \\
g_{pp} &= \left\{-2eh\beta^2(1-m)^2\left[1 + h\beta(1-m)P^*\right]^{-3} + \frac{2}{9}e\rho P^{*-\frac{4}{3}}\right\}Z^*, \\
g_{pz} &= e\beta(1-m)\left[1 + h\beta(1-m)P^*\right]^{-2} + \frac{2}{3}e\rho P^{*-\frac{1}{3}}, \\
f_{ppp} &= -6ch^2\beta^3(1-m)^3\left[1 + h\beta(1-m)P^*\right]^{-4}Z^*, \\
f_{ppz} &= 2ch\beta^2(1-m)^2\left[1 + h\beta(1-m)P^*\right]^{-3}, \\
g_{ppp} &= \left\{6eh^2\beta^3(1-m)^3\left[1 + h\beta(1-m)P^*\right]^{-4} - \frac{8}{27}e\rho P^{*-\frac{7}{3}}\right\}Z^*, \\
g_{ppz} &= -2eh\beta^2(1-m)^2\left[1 + h\beta(1-m)P^*\right]^{-3} + \frac{2}{9}e\rho P^{*-\frac{4}{3}}.
\end{aligned}$$

In the following, we calculate $W_{20}(\theta)$ and $W_{11}(\theta), \theta \in [-1,0]$ to obtain g_{21}. According to (3.15),

$$\dot{W}(z,\bar{z}) = W_{20}(\theta)z\dot{z} + W_{11}(\theta)\dot{z}\bar{z} + W_{11}(\theta)z\dot{\bar{z}} + W_{02}(\theta)\bar{z}\dot{\bar{z}} + \cdots, \tag{3.18}$$

$$A_{\bar{\tau}}W = A_{\bar{\tau}}W_{20}(\theta)\frac{z^2}{2} + A_{\bar{\tau}}W_{11}(\theta)z\bar{z} + A_{\bar{\tau}}W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. \tag{3.19}$$

It is known that $\dot{W}(z,\bar{z})$ satisfies

$$\dot{W} = A_{\bar{\tau}}W + H(z,\bar{z}), \tag{3.20}$$

and one has

$$\dot{W} = \dot{p}_t - \dot{z}pb_n - \dot{\bar{z}}\bar{p}b_n = \begin{cases} W - 2\operatorname{Re}\{g(z,\bar{z})p(\theta)\}b_n, & \theta \in [-1,0), \\ A_{\bar{\tau}}W - 2\operatorname{Re}\{g(z,\bar{z})p(\theta)\}b_n + \tilde{F}, & \theta = 0, \end{cases} \tag{3.21}$$

$$H(z,\bar{z},\theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots.$$

Obviously,

$$H_{20}(\theta) = \begin{cases} -g_{20}p(\theta)b_n - \bar{g}_{02}\bar{p}(\theta)b_n, & \theta \in [-1,0), \\ -g_{20}p(0)b_n - \bar{g}_{02}\bar{p}(0)b_n + \tilde{F}''_{zz}, & \theta = 0, \end{cases}$$

$$H_{11}(\theta) = \begin{cases} -g_{11}p(\theta)b_n - \bar{g}_{11}\bar{p}(\theta)b_n, & \theta \in [-1,0), \\ -g_{11}p(0)b_n - \bar{g}_{11}\bar{p}(0)b_n + \tilde{F}''_{z\bar{z}}, & \theta = 0. \end{cases}$$

According to Eqs. (3.18) and (3.21),

$$(A_{\bar{\tau}} - 2i\omega_0\bar{\tau})W_{20}(\theta) = -H_{20}(\theta), \qquad A_{\bar{\tau}}W_{11}(\theta) = -H_{11}(\theta), \qquad \ldots. \tag{3.22}$$

Computing we have

$$\begin{aligned} W_{20}(\theta) &= -\frac{g_{20}}{i\omega_n\bar{\tau}}p(0)e^{i\omega_n\bar{\tau}\theta}b_n - \frac{\bar{g}_{02}}{3i\omega_n\bar{\tau}}\bar{p}(0)e^{-i\omega_n\bar{\tau}\theta}b_n + E_1e^{2i\omega_n\bar{\tau}\theta}, \\ W_{11}(\theta) &= \frac{g_{11}}{i\omega_n\bar{\tau}}p(0)e^{i\omega_n\bar{\tau}\theta}b_n - \frac{\bar{g}_{11}}{i\omega_n\bar{\tau}}\bar{p}(0)e^{-i\omega_n\bar{\tau}\theta}b_n + E_2. \end{aligned} \tag{3.23}$$

When $\theta = 0$, by (3.22) and (3.23), we get

$$(2i\omega_n\bar{\tau} - A_{\bar{\tau}})E_1e^{2i\omega_n\bar{\tau}\theta}\big|_{\theta=0} = F_{20}b_n^2, \qquad A_{\bar{\tau}}E_2\big|_{\theta=0} = -F_{11}b_n^2,$$

in which

$$\begin{aligned} F_{20} &= \left(F_{20}^{(1)}, F_{20}^{(2)}\right)^T = \begin{pmatrix} f_{pp} + 2f_{pz}a + 2f_{pp_t}e^{-i\omega_n\bar{\tau}} \\ g_{pp} + 2g_{pz}a \end{pmatrix}, \\ F_{11} &= \left(F_{11}^{(1)}, F_{11}^{(2)}\right)^T = \begin{pmatrix} f_{pp} + f_{pz}(a+\bar{a}) + f_{pp_t}(e^{i\omega_n\bar{\tau}} + e^{-i\omega_n\bar{\tau}}) \\ g_{pp} + g_{pz}(a+\bar{a}) \end{pmatrix}. \end{aligned}$$

Suppose that $b_n^2 = \sum_{n=1}^{\infty} c_nb_n$, in which c_n are the coordinates. We have

$$\begin{aligned} E_1 &= \sum_{n=1}^{\infty}\left(2i\omega_n + \mu_nD - L_1 - L_2e^{-2i\omega_n\bar{\tau}}\right)^{-1}F_{20}c_nb_n, \\ E_2 &= \sum_{n=1}^{\infty}(\mu_nD - L_1 - L_2)^{-1}F_{11}c_nb_n, \end{aligned}$$

where

$$\begin{aligned} &\left(2i\omega_n + \mu_nD - L_1 - L_2e^{-2i\omega_n\bar{\tau}}\right)^{-1} \\ &\quad = \frac{1}{\kappa_1^n}\begin{pmatrix} 2i\omega_n + d_2\mu_n & f_z \\ g_p & 2i\omega_n + d_1\mu_n - f_p - f_{p_t}e^{-2i\omega_n\bar{\tau}} \end{pmatrix}, \\ &(\mu_nD - L_1 - L_2)^{-1} = \frac{1}{\kappa_2^n}\begin{pmatrix} d_2\mu_n & f_z \\ g_p & d_1\mu_n - f_p - f_{p_t} \end{pmatrix}, \end{aligned}$$

$$\kappa_1^n = -4\omega_n{}^2 - f_z g_p - 2i\omega_n\bigl(f_p + f_{p_t} e^{-2i\omega_n\bar{\tau}}\bigr)$$
$$\quad - d_2\bigl(f_p + f_{p_t} e^{-2i\omega_n\bar{\tau}}\bigr)\mu_n + d_1 d_2 \mu_n^2 + 2i\omega_n(d_1 + d_2)\mu_n,$$
$$\kappa_2^k = -f_z g_p - d_2(f_p + f_{p_t})\mu_n + d_1 d_2 \mu_n^2.$$

Now, all the unknown terms in (3.17) are represented, therefore, we can compute the following values:

$$c_1(0) = \frac{1}{2\omega_n\bar{\tau}}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2},$$
$$\mu_2 = -\frac{\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\bar{\tau}))},$$
$$\beta_2 = 2\operatorname{Re}\bigl(c_1(0)\bigr),$$
$$P_2 = -\frac{1}{\omega_n\bar{\tau}}\bigl[\operatorname{Im}\bigl(c_1(0)\bigr) + \mu_2 \operatorname{Im}\bigl(\lambda'(\bar{\tau})\bigr)\bigr].$$

Theorem 3.2 *For $\tau > \bar{\tau} = \tau_n^{j,\pm}$ ($\tau < \bar{\tau} = \tau_n^{j,\pm}$), we obtain the following properties of Hopf bifurcation*:

(i) *If $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical* (*subcritical*), *and bifurcating periodic solutions exist*;

(ii) *If $\beta_2 < 0$ ($\beta_2 > 0$), the bifurcating periodic solutions are stable* (*unstable*) *on the central manifold*;

(iii) *If $P_2 > 0$ ($P_2 < 0$), the period of the periodic solutions increases* (*decreases*).

4 Conclusions and biological significance

In this paper, the formulae for determining the direction of Hopf bifurcation and the stability of periodic solutions are given by using the normal form method and central manifold theory. The corresponding numerical simulations are carried out. For the case with nonlocal production delay, by analyzing the distribution of characteristic roots, it can be concluded that the trivial steady-state solution and the boundary equilibrium have the same local stability as in the case with a discrete delay, the system has a stability switch, and the constant equilibrium switches finitely many times from stable to unstable, then from unstable to stable, finally becoming unstable.

The equilibrium $E_1 = (K, 0)$ means that when the phytoplankton reaches the environmental carrying capacity, i.e., the zooplankton has sufficient food, the death rate of zooplankton is greater than its individual growth rate, the zooplankton population will eventually become extinct, and the phytoplankton population will eventually stabilize at the maximum carrying capacity of the environment. When the coexisting positive equilibrium $E^* = (P^*, Z^*)$ exists, the research shows that the delay will affect the stability of the system, which can make a stable positive equilibrium become unstable, thus generate a Hopf bifurcation. Biologically, the outbreak of plankton population can be controlled by controlling the time of toxin attack. Due to the introduction of a diffusion term and production delay, the system may have spatially homogeneous or nonhomogeneous periodic solutions. That is to say, under the low intensity of marine habitat complexity effect, if the predator's predation ability is low and there is a low production delay, then the predator and prey can coexist in time and space, and the size of the population will remain near the stable value.

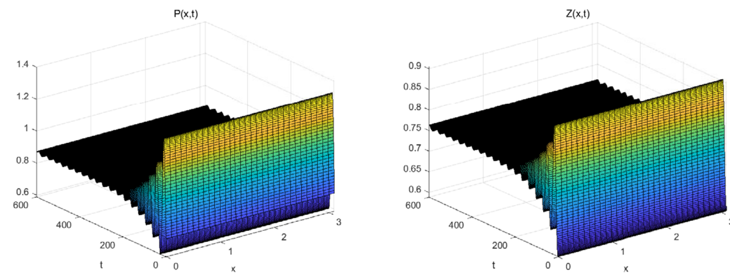

Figure 1 If $m = 0.6$, the equilibrium $E^* = (0.866, 0.757)$ is locally asymptotically stable

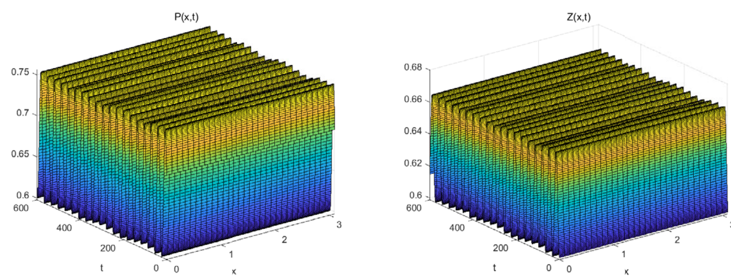

Figure 2 If $m = 0.5$, the stable periodic solutions bifurcate from the equilibrium $E^* = (0.866, 0.757)$

5 Numerical simulations

In this section, we give some numerical simulations to verify the correctness of conclusions.

(1) Stability of the diffusion system without delay caused by habitat complexity

Example 1 In system (2.1), we choose parameters

$$r = 0.5, \quad K = 5, \quad c = 0.4, \quad \beta = 4, \quad m = 0.6,$$
$$e = 0.1, \quad \mu = 0.1, \quad \rho = 0.2, \quad h = 0.125.$$

Let $d_1 = 1$, $d_2 = 0.5$, and select m as the bifurcation parameter to verify the stability of the reaction–diffusion equation. Taking $m = 0.6$, we get $E^* = (P^*, Z^*) = (0.866, 0.757)$. By Theorem 2.3, when $m > m_0 = 0.5736$, the system is locally asymptotically stable at $E^* = (P^*, Z^*)$ (shown in Fig. 1). Taking $m = 0.5$, when $m < m_0 = 0.5736$, the system is unstable at $E^* = (P^*, Z^*)$ (shown in Fig. 2).

(2) Stability switch of the system induced by delay

Example 2 Let $\Omega = (0, 2\pi)$, i.e., $l = 2$. Take parameters as

$$d_1 = 1, \quad d_2 = 2, \quad r = 0.5, \quad K = 5, \quad c = 0.4, \quad \beta = 4,$$
$$m = 0.6, \quad e = 0.1, \quad \mu = 0.1, \quad \rho = 0.2, \quad h = 0.125.$$

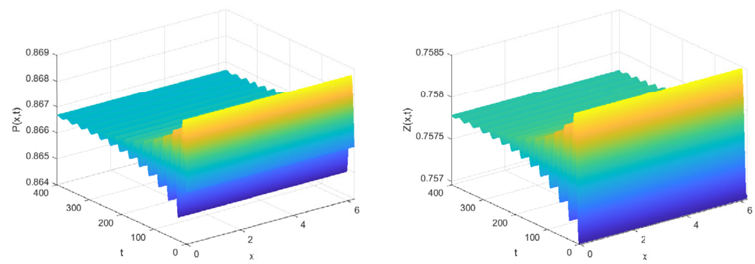

Figure 3 If $\tau = 2$, the equilibrium $E^* = (0.866, 0.757)$ is locally asymptotically stable

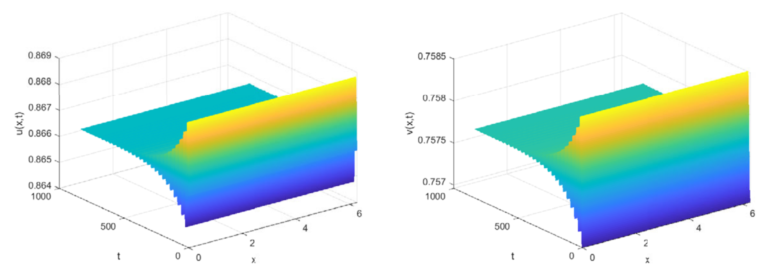

Figure 4 If $\tau = 4$, the equilibrium $E^* = (0.866, 0.757)$ is locally asymptotically stable

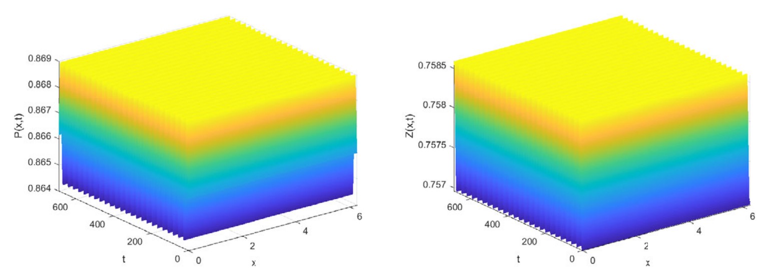

Figure 5 If $\tau = 3.45$, the stable periodic solutions bifurcate from the equilibrium $E^* = (0.866, 0.757)$

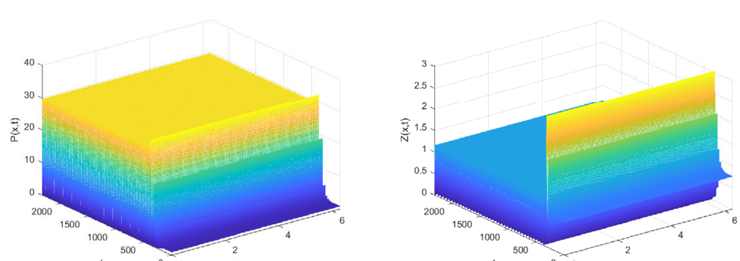

Figure 6 If $\tau = 5.8$, the stable periodic solutions bifurcate from the equilibrium $E^* = (0.866, 0.757)$

Calculating we get $E^* = (P^*, Z^*) = (0.866, 0.757)$, $\tau_1^{0,+} \doteq 2.873 < \tau_1^{0,-} \doteq 3.617 < \tau_1^{1,+} \doteq 5.126$. According to our theorem, when $\tau \in (0, \tau_1^{0,+}) \cup (\tau_1^{0,-}, \tau_1^{1,+})$, $E^* = (P^*, Z^*)$ is locally asymptotically stable (shown in Figs. 3 and 4), when $\tau \in (\tau_1^{0,+}, \tau_1^{0,-}) \cup (\tau_1^{1,+}, +\infty)$, $E^* = (P^*, Z^*)$ is unstable (shown in Figs. 5 and 6). When τ crosses $\tau_1^{0,\pm}$, the equilibrium $E^* = (P^*, Z^*)$ loses stability and a Hopf bifurcation occurs. By Theorem 3.3,

$$\mu_2 \approx 2.5305 > 0, \qquad \beta_2 \approx -0.2637 < 0, \qquad P_2 \approx 0.4371 > 0.$$

Therefore, the bifurcating periodic solutions are asymptotically stable, and the period increases.

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Declarations

Competing interests
The author declares that they have no competing interests.

Authors' contributions
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